

RESPONSE SPECIFICITY IN ANIMAL TIMING

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The stimuli that control responding in the peak procedure were investigated by training rats, in separate sessions, to make two different responses for food reinforcement. During one type of session, lever pressing was normally reinforced 32 s after the onset of a light. During the other type of session, chain pulling was normally reinforced either 8 s after the onset of one auditory cue or 128 s after the onset of a different auditory cue. For both types of sessions, only the appropriate manipulandum was available, and 20% of the trials lasted 240 s and involved no response-contingent consequences. Rats were then tested with the auditory cues in the presence of the lever and the light in the presence of the chain. If the time of reinforcement associated with each stimulus was learned, response rates should peak at these times during transfer testing. However, if a specific response pattern was learned for each stimulus, little transfer should occur. The results did not clearly support either prediction, leading to the conclusion that both a representation of the time of reinforcement and the rat's own behavior may control responding in this situation.

Key words: timing, peak procedure, transfer, internal clock, lever press, chain pull, rats

Animals successfully discriminate temporal durations on the order of seconds to minutes (e.g., Catania, 1970; Church, 1984; Church & Gibbon, 1982; Gibbon, Church, & Meck, 1984; Killeen & Fetterman, 1988; S. Roberts, 1981; W. Roberts, Cheng, & Cohen, 1989). Such time discriminations may depend on the animal's perception of time directly (Gibbon et al., 1984) or may be behaviorally mediated (Killeen & Fetterman, 1988). The purpose of the present experiment was to investigate the nature of what is learned in one particular timing task, the peak procedure (S. Roberts, 1981). The peak procedure involves training subjects with two kinds of trials. Each trial begins with the onset of some stimulus (e.g., a light). On some trials, the first target response made after a fixed period of time from the onset of the stimulus produces reinforcement

and terminates the stimulus. These trials correspond to a discrete-trial fixed-interval (FI) schedule. On the second type of trial, no food can be earned. The stimulus is presented for a much longer period, and the subject's responses have no scheduled effect. These no-food trials will be referred to as empty trials (S. Roberts, 1981).

The pattern of responding on empty trials indicates sensitivity to the time of reinforcement on FI trials. Specifically, mean response rate on empty trials accelerates to a peak at about or slightly beyond the FI value and then decreases. Whether this pattern reflects the animal's comparison of remembered FI time with perceived elapsed time (Church, 1984; Meck & Church, 1982; S. Roberts, 1981) or whether it reflects control through a mediating behavioral chain (Killeen & Fetterman, 1988) is open to question.

Church (1984), Gibbon (1986), and their colleagues (e.g., Meck, 1983; S. Roberts, 1982) have proposed an information-processing model of timing in which responding in the peak procedure is based on a comparison between perceived elapsed time on the current trial and a memory for the time of reinforcement. Elapsed time is monitored by a clock mechanism, consisting of a pacemaker, a switch, and an accumulator. Onset of the FI signal closes the switch between the pacemaker and the accumulator, allowing pulses to enter the accumulator. Prior to reinforcement, the

The data reported here were collected at the Department of Experimental Psychology, University of Cambridge, England. Data analysis and preparation of this manuscript were supported by Canadian National Science and Engineering Research Council Grant OGP0037341 to the first author. We wish to thank Tony Dickinson for the use of his apparatus and his helpful comments on this work and Lorraine Allan, Russ Church, John Gibbon, Warren Meck, and Seth Roberts for their comments on an earlier version of this manuscript. Special thanks are given to Ron Racine for his graphics expertise. Correspondence concerning this paper should be sent to the first author at the Department of Psychology, McMaster University, 1280 Main St. West, Hamilton, Ontario L8S 4K1, Canada.

accumulated value is repeatedly checked against a reference memory value, and, if their ratio falls below some threshold value, a response is made; otherwise, no response is made. At the time of reinforcement, the accumulated value is stored in reference memory. Variance and distortion can occur in the different components of this system. For example, there may be some (nonconstant) latency for a signal to close the switch between the pacemaker and the accumulator (Meck, 1984) and some modification of the temporal representation during transfer from accumulator to reference memory (Gibbon et al., 1984).

In contrast to this information-processing model, Killeen and Fetterman (1988) have proposed a theory more in keeping with a traditional behavior-analytic framework. They suggested that temporal discrimination learning involves the development of conditional discriminations in which the animal's own behavior can act as a discriminative stimulus for subsequent responses. To explain responding on the peak procedure, they suggest that types of adjunctive behavior become shaped into a behavioral chain that terminates in the instrumental response. Pulses from an internal pacemaker, with a rate of output dependent on the rate of reinforcement, lead to progression through the behavioral chain.

The present experiment attempts to distinguish these alternatives by training rats on multiple-peak procedures with unique stimuli and responses and then testing novel stimulus-response combinations. Consider rats trained with two different stimuli, each signaling different FI schedules. If the instrumental response required for reinforcement is the same for both stimuli, responding will come to peak at the appropriate time for each one (S. Roberts, 1981; W. Roberts et al., 1989). Suppose that the instrumental response required for reinforcement is different for each stimulus. For example, during some sessions, a lever might be available and a lever press could produce food after 32 s in the presence of a light. During other sessions, a chain might be available and a chain pull could earn food after 8 s in the presence of a tone. Once the appropriate peak patterns developed for each, how would rats respond to the tone in the presence of the lever? If performance is based on a comparison of elapsed time (from tone onset) with remembered FI time (for the tone), lever press-

ing should peak at around 8 s. In contrast, if performance is based on the conditionality of behavioral states, responding should be relatively unsystematic, because necessary behavioral supports (e.g., the chain) are absent.

The present experiment was somewhat more complicated than the one described above. As in the hypothetical experiment described above, rats were trained to press a lever to earn food on an FI 32-s schedule, signaled by a light. During other sessions, the lever was removed from the experimental chamber and a chain was inserted. Under these conditions, the same rats experienced two auditory stimuli, one correlated with an FI 8-s schedule, the other correlated with an FI 128-s schedule. After training, rats were tested with the auditory stimuli in the presence of the lever, and, subsequently, with the light in the presence of the chain.

There were several reasons for training the rats such that responding to two transfer stimuli could be assessed in the presence of the lever. First, even if transfer responding did not conform to a standard peak pattern in time, an influence of prior training history might still be detected if responding in the presence of the two auditory cues differed. Second, once differential chain responding was established to the two during training, identical transfer responding to the auditory stimuli could not be interpreted as a failure to discriminate their associated FI values. In contrast, with only a single transfer stimulus, failure to discriminate the FI values associated with the light and that stimulus would be a possible interpretation if lever pressing to the two were similar. Finally, and perhaps most importantly, training on two different FI schedules in the presence of the chain should encourage the signals to gain greater control over responding than the manipulandum cues.

Given the assumption that the FI cue alone controls retrieval of a reference memory value, the information-processing model clearly predicts that lever pressing in the presence of the auditory cues should track their FI values (peaks at 8 and 128 s for the two auditory cues). The information-processing model does not explicitly specify the cues that control retrieval from reference memory, however; if other cues were to influence retrieval, the predicted outcome of the transfer test would be different. For example, it is possible that, as a result of separate training with only one FI

value in the presence of each manipulandum, the manipulandum cues themselves would gain control over retrieval. In the extreme, the FI cue might have no control over retrieval and may function only to close the switch between pacemaker and accumulator (initiate timing). In a transfer test with tone and lever, lever cues would retrieve the FI value experienced during lever-press training, causing lever pressing to peak close to 32 s.

A less extreme possibility is that the FI cues and the manipulandum cues jointly control retrieval. As a result of training, both the light and the lever cues could become associated with a reinforcement time of 32 s. This could lead to one of two intermediate results when the auditory cues and lever occur together for the first time. The auditory cue should retrieve its FI value (8 or 128 s), but the lever might retrieve its FI value (32 s). If the two retrieved times were averaged, lever pressing might peak between the time appropriate to the cue and the time appropriate to the lever. Alternatively, two peaks in responding might occur, one at the time appropriate for the cue and one at the time appropriate for the lever (e.g., Meck & Church, 1984).

METHOD

Subjects

The subjects were 8 male hooded Lister rats. They had previously been trained to lever press and chain pull on random-interval 60-s schedules for liquid sucrose reward. They had no previous exposure to the visual or auditory stimuli used in the present experiment. Throughout the present experiment they were housed in pairs and maintained at 80% of their free-feeding weights. One rat died during the course of the experiment; his data were therefore excluded from this report.

Apparatus

The experiment was carried out using four modified Campden Instruments rat operant chambers, housed inside sound- and light-attenuating shells. One wall of each chamber contained an aperture into which could be delivered 45-mg food pellets (Abels Laboratory, Formula 1). A retractable lever was located to the left of the food aperture, and a speaker, through which an 1800-Hz tone could be presented, was located to the right of the aperture.

A 3-W light was located in the center of this wall, above the aperture. A heavy-duty relay located behind this wall, when operated at a rate of 1.5 Hz, produced a clicking noise. A chain, suspended from a microswitch, could be inserted into the chamber through a hole located in the center of the ceiling. Throughout the experiment, only one manipulandum, lever or chain, was present in the box at any given time. When the chain was present, a metal plate covered the hole into which the lever was retracted.

Procedure

Because of the subjects' prior experimental history, no shaping was required. Subjects were given discrete-trial lever-press training on an FI 32-s schedule, with trials signaled by the onset of the light. The first lever press occurring 32 s after light onset produced delivery of a food pellet as well as light offset. Sessions consisted of 50 trials, presented with a fixed intertrial interval (ITI) of 5 s during the first session and a variable ITI averaging 40 s during subsequent sessions. Beginning with the third session, 10 of the 50 trials were empty trials. On empty trials, the light remained on for 240 s and lever presses had no scheduled effects. The sequence of FI and empty trials was random and changed daily.

After 20 sessions as described above, the lever was retracted from the box and the chain inserted. During the first chain-pull session, rats were allowed to pull 50 times, with each pull earning a food pellet. Rats were then exposed to a multiple schedule in which the tone and clicker were uniquely correlated with FI 8-s and FI 128-s schedules. For Rats 1, 2, and 4, the tone signaled FI 8 s and the clicker signaled FI 128 s; for the rest, the opposite arrangement held. Each session contained 20 FI 8-s and 20 FI 128-s trials, interspersed with 10 empty trials, five with the tone and five with the clicker. On empty trials, chain pulling had no scheduled consequences. The sequence of FI and empty trials was determined by a microprocessor's random number generator and changed daily.

After rats had received 20 sessions with the tone and clicker, sessions with the lever were reintroduced. Every block of six sessions contained four chain and two lever sessions, presented in different orders over blocks. Whenever the lever was present, the chain was

removed from the box, and vice versa. Otherwise, procedures continued as before: During lever sessions, the light signaled an FI 32-s schedule; during chain sessions, the auditory cues signaled FI 8-s and FI 128-s schedules. Each session contained 10 empty trials. This training continued until the rats had received a total of 30 lever and 40 chain sessions.

At this point, rats were responding with a clear peak pattern on FI 8-s trials but not on FI 128-s trials. Therefore, to give rats more experience with the FI 128-s schedule, the proportion of FI 8-s and FI 128-s trials in each chain session was changed. Chain sessions were still given twice as often as lever sessions, but now chain sessions contained only four FI 8-s trials, with one corresponding empty trial, and 36 FI 128-s trials, with nine corresponding empty trials. After rats had received a total of 40 lever sessions and 60 chain sessions, the number of FI 8-s and FI 128-s trials in each chain session was returned to 20 each (with five corresponding empty trials of each type). Rats were given an additional two lever and four chain sessions.

A series of four transfer tests in the presence of the lever was then conducted. These tests were intermixed with chain sessions such that each test session was preceded by two standard chain sessions. Each transfer test in the presence of the lever contained 41 FI 32-s trials signaled by the light (as in lever training sessions) and nine 240-s empty trials, three each with the light, tone, and clicker. Thus, for the first time, the tone and clicker were presented in the presence of the lever. Presentation of empty trials was constrained such that they never occurred as one of the first 11 trials, and each type occurred once in each subsequent block of 13 trials. (Specifically, Trials 12, 16, 20, 26, 30, 34, 40, 44, and 48 were designated as empty trials, with presentation order of the three cues different in each session.)

A series of four transfer tests in the presence of the chain was then conducted. These tests

were intermixed with standard chain and lever training sessions (seven chain and six lever sessions) and were always immediately preceded by a standard lever session and immediately followed by a standard chain session. Each transfer test in the presence of the chain contained 49 trials. The first 10 consisted of five FI 8-s and five FI 128-s trials signaled by the appropriate auditory stimuli; the remaining three blocks of 13 trials each contained five FI 8-s, five FI 128-s, and three empty trials (one each of the light, tone, and clicker). Specifically, empty trials occurred on Trials 13, 17, 21, 26, 30, 34, 39, 43, and 47, with presentation order of the three cues different in each session. Thus, for the first time the light occurred in the presence of the chain.

RESULTS

Data from the end of training, the first lever test session, and the first chain test session are shown in Figure 1. These graphs show responding during successive 8-s periods of the 240-s empty trials, expressed as percentage of maximum responding. Percentage of maximum was calculated by finding, for each stimulus, the 8-s period with the maximum average response rate (averaged over trials), and then multiplying the average rate for each period of that stimulus by 100/maximum. The actual maximums used in these calculations, in responses per minute, are presented above the 100% point of each curve.

The left graph in each row shows responding averaged over the last 10 empty trials with each stimulus from the final sessions of training. For all rats except Rat 1, maximum rate of lever pressing during light trials (FI 32) was higher than maximum rate of chain pulling during tone or clicker trials. Higher lever-pressing than chain-pulling rates are typical in this specific apparatus, even when the two responses provide reinforcement according to identical schedules (e.g., Dickinson & Daw-

Fig. 1. Responding during successive 8-s periods of the 240-s long empty trials, expressed as percentage of maximum rate, for each stimulus. Percentage of maximum was calculated by finding, for each stimulus, the 8-s period with the maximum average response rate (averaged over trials) and then multiplying the average rate for each period of that stimulus by 100/maximum. The actual maximums used in these calculations, in responses per minute, are presented above the 100% point of each curve. End-of-training (left column) data are based on 10 trials with each stimulus; lever-test (center column) and chain-test (right column) data are based on three trials with each. Responding during the FI 32-s stimulus is represented by the continuous line, responding during the FI 8-s stimulus by the solid bars, and responding during the FI 128-s stimulus by the open bars.

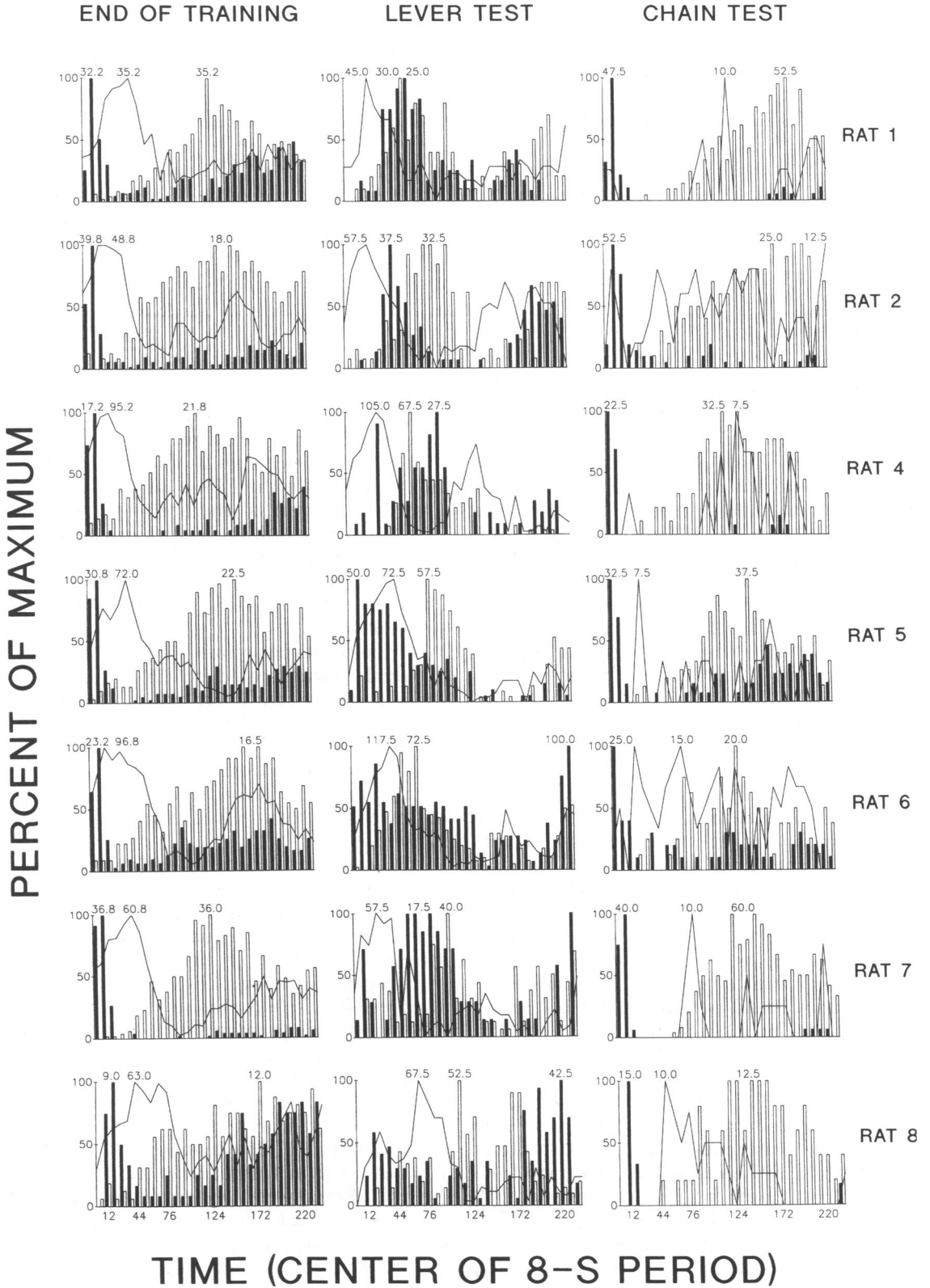


Table 1
Peak time (center of 8-s period).

Rat	End of training			Lever Test 1			Chain Test 1		
	FI 32	FI 8	FI 128	FI 32	FI 8	FI 128	FI 32	FI 8	FI 128
1	44	20	148	36	68	76	220	12	188
2	28	12	148	28	60	92	124	12	172
4	28	12	140	36	84	84	148	4	148
5	44	12	156	44	36	100	108	4*	148
6	36	12*	164	44	60	68	108	4	132
7	36	12	140	36	76	116	140	12	156
8	60	20*	172	68	196	124	84	12	148
Mean	39.5	14.3	152.6	41.7	82.8	94.3	133.1	8.6	156.0
Median	36.0	12.0	148.0	36.0	68.0	92.0	124.0	12.0	148.0

* Calculated over the first 120 s only.

son, 1987). Nevertheless, expressing these rates as percentage of maximum rate shows responding characteristic of the peak procedure. During each stimulus, responding tended to increase and reach a peak just beyond the time at which food could be earned on FI trials and to decrease thereafter. In addition, the broadness of the peaks tended to increase with increasing FI values. There was also a tendency for responding to increase toward the end of the 240-s trials, a pattern that is characteristic of this procedure when empty trials are long relative to the ITI (W. Meck, personal communication).

The left section of Table 1, labeled "end of training," shows peak times (calculated in a similar manner to S. Roberts, 1981) for each rat, using the data from the last 10 empty trials of training with each stimulus. Peak time is a derived measure that does not necessarily correspond to the period with the maximum response rate, but rather gives the center of the highest region of the response distribution in time. Peak time was calculated taking medians over increasingly restricted portions of the response distribution such that each successive median was found over the range of periods for which the previous median was the center. When two successive medians agreed, the period of that median was taken as the peak time. For example, Rat 5 made a total of 1,084 responses to the light over the 10 trials used to calculate peak time for the end of training. The median, 542, was located in Period 9, so the total responses for Periods 1 through 18 were found (779). The new median, 389.5, fell in Period 6, so the next total was taken over Periods 1 through 12. This total was 667,

making the new median 333.5, which also fell in Period 6, so the center of this period (44 s) was taken as the peak time. In certain cases, this method yielded an inappropriate result. In particular, for the FI 8-s distribution, with a very sharp peak at the beginning followed by a long rising tail, the measure of peak time sometimes fell in the last 120 s of the distribution; in these cases peak time was derived using the first 120 s of the distribution only (see Table 1).

For most rats peak time fell close to the time at which reward could be earned on corresponding FI trials. There was no overlap in the distributions of these scores for the three stimuli; that is, all peak times derived for the FI 8-s cue were lower than all peak times derived for the FI 32-s cue, which in turn were all lower than peak times derived for the FI 128-s cue.

Although four transfer test sessions were conducted in the presence of each manipulum, only data from the first transfer test with each are presented, because the pattern of responding tended to change unsystematically with repeated testing. The data for the first lever test, in which the auditory FI 8-s and FI 128-s cues were presented for the first time in conjunction with the lever, are shown in the center column of Figure 1. These graphs show percentage of maximum for each of the three signals averaged over the three empty trials given with each. The middle panel of Table 1 shows the peak times derived from the lever test data. Responding to the light (FI 32-s cue) continued to peak shortly beyond 32 s. This was hardly surprising, because the rats were trained with this stimulus in the presence of

the lever. Of more interest was the pattern of transfer responding to the FI 8-s and FI 128-s cues. Inspection of the center column of Figure 1 reveals that the response distributions for these stimuli (bars) did display a "peakedness"; but there was far less consistency across rats than for the light, in terms of the location and sharpness of the peaks.

For every rat, peak time for the FI 8-s cue occurred later than it had at the end of training, whereas peak time to the FI 128-s cue occurred earlier than it had during training. An analysis of the peak times from Lever Test 1 yielded a reliable effect of stimulus, $F(2, 12) = 8.09$; $p < .01$. Pairwise comparisons using the Newman-Keuls method indicated that peak times for both the FI 8-s and FI 128-s cues were reliably greater than that for the FI 32-s cue, but that they did not differ from one another.

Despite the failure of the peak times for the FI 8-s and FI 128-s cues to differ significantly, an analysis of variance carried out for the first 120 s of the data indicated that the rats did respond to each of them with different patterns over time. The interaction between stimulus type and 8-s time period was statistically significant, $F(14, 84) = 2.09$; $p < .05$. When each cue was examined separately, responding to the FI 128-s cue was found to vary reliably as a function of 8-s time period, $F(14, 84) = 3.5$; $p < .01$, but responding to the FI 8-s cue did not, $F(14, 84) = 1.71$; $p = .068$.

Examination of the graphs of individual subjects suggests some degree of transfer, in that, except for Rat 1, rats responded differently to the two auditory cues. However, the nature of this transfer is unclear, because there was little consistency in the pattern of responding across rats. Rat 2 produced a peaked distribution to each cue, with the maximum for the FI 128-s cue later than for the FI 8-s cue; but the maxima for both of these was later than the maximum for the FI 32-s cue. Rat 4 also produced a peaked distribution to each cue, with both maxima falling above that of the FI 32-s cue; but for Rat 4, the maximum for the FI 8-s cue was later than for the FI 128-s cue. In addition, for the FI 8-s cue, there was a brief spurt of responding in the same time period that the FI 32-s cue evoked maximum responding. Rat 5 produced peaked response distributions that fell on the appropriate sides of 32 s and were remarkably similar in shape. Maximum for the FI 8-s cue oc-

curred in the same time period as it did at the end of training; however, lever pressing after this point declined much more gradually than did chain pulling (compare solid bars across left and center columns). Rat 6 produced a peaked distribution to the FI 128-s cue with the maximum between 32 and 128 s; in contrast, the response distribution to the FI 8-s cue was relatively flat over the first 120 s. Rat 7 produced complex distributions to each transfer cue. For the FI 128-s cue, there was a peak between 32 and 128 s, but there was also a suggestion of a lower peak closely located to the peak for the FI 32-s cue. For the FI 8-s cue there was an early burst of responding, appropriate to the FI 8-s cue, but this was followed by a broader, higher peaked distribution, centered around 76 s. Rat 8 also produced complicated distributions, including an aberrant pattern to the FI 32-s cue. The curve for the FI 128-s cue appears to have two peaks, one shortly before and one shortly after 128 s. The curve for the FI 8-s cue tends to track that for the FI 32-s cue for about the first 48 s, but diverges from it thereafter. In summary, all of the rats tended to show some sort of a peaked response distribution to the FI 128-s cue, with the peak falling between 32 and 128 s; rats differed in their reaction to the FI 8-s cue, producing response distributions that peaked before that of the FI 32-s cue (Rats 5 and 8), between those of the FI 32-s and FI 128-s cues (Rats 2 and 7), about the same time or even after that of the FI 128-s cue (Rats 1 and 4, respectively), or not at all (Rat 6).

The data for the first chain test, in which the light (FI 32-s cue) was presented for the first time in conjunction with the chain, are shown in the right column of Figure 1. Each graph shows percentage of maximum rate of chain pulling to each of the three signals averaged over the three empty trials given with each. Rats continued to respond appropriately to the FI 8-s and FI 128-s cues, whereas responding to the FI 32-s transfer cue was low and erratic. There was no reliable effect of time period on responding in the presence of the light, $F(29, 174) = 1.09$; $p > .3$. Rat 2 responded to the light with a pattern resembling a conglomeration of the distributions to the auditory cues. Rat 8 produced an asymmetric peaked distribution located relatively close to that which it normally produced to the light while lever pressing. For the remaining

rats, there was little evidence of systematic responding.

The right panel of Table 1, labeled "Chain Test 1," shows the peak times derived from these data. Responding to the FI 32-s cue did not resemble the form of standard peak-procedure results; however, peak times were calculated by the standard method for the sake of completeness. For 5 of the 7 rats, the resulting peak time was simply the median of the response distribution. For every rat, peak time for the FI 32-s cue with the chain was greater than it had been at the end of training with the lever.

DISCUSSION

Schedule-appropriate response patterns developed with multiple-peak procedure training. With the stimulus-response combinations used in training, the different stimuli controlled different patterns of responding over the course of the empty trials. This control was detectable with as few as three trials; that is, during the transfer test sessions, responding to the nontransfer stimuli continued to conform to the pattern established in training.

When stimuli and responses were recombined in the lever test, responding did not conform to any of the potential outcomes discussed in the introduction. Responding to the transfer FI 8-s and FI 128-s cues did not resemble the pattern of responding those cues evoked on the chain, nor did it resemble the pattern of responding evoked by the light. The possibility that responding was determined by an average of the times associated with the cue and the manipulandum seems plausible for the FI 128-s cue but not the FI 8-s cue. Responding to the FI 128-s cue tended to peak between 32 and 128 s; however, responding to the FI 8-s cue tended to peak later than 32 s, instead of between 8 and 32 s. Double peaks, one at the time associated with the cue and one at the time associated with the lever, were not apparent either. Thus, none of the straightforward predictions from the information-processing model were supported. The claim that the only thing rats learned during training was a different behavioral sequence for each cue also seems unattractive, however, for if this were correct, transfer responding should have been similar to the two cues and completely unsystematic.

The idiosyncratic transfer responding observed in the lever test may have been due to joint control by the explicit signal present and the manipulandum cues present. Because only one FI schedule was trained in the presence of the lever, it is possible that lever cues (or cues produced by lever pressing) gained some discriminative control. The ability of the light to overshadow lever-related cues may have differed across rats (Reynolds, 1961). In addition, lever-related cues could only exert control once a rat has made contact with them. Thus, the different patterns observed could have been partially determined by differences in when during a trial rats entered the vicinity of the lever. Suppose that when the transfer stimuli were presented, they initiated the rats' "normal" behavior pattern, either by initiating a behavioral chain or retrieving a temporal value from reference memory. For the FI 8-s cue, both should immediately provoke approach to the chain; but because the chain was absent, the rats could not continue with their habitual pattern. Contact with the lever cues might have influenced the pattern of subsequent responding, but the time of this contact would have been different for different rats. For the FI 128-s cue, initial behavior did not involve the chain and may have provided the opportunity for the rats to come into contact with the lever before they would normally have approached the chain. In the context of the information-processing model, perhaps averaging two conflicting times of reinforcement depends on retrieving both those times prior to either one having elapsed. Although clearly ad hoc, this explanation might account for why an averaging explanation fits the FI 128-s cue results but not the FI 8-s cue results.

Unlike in the lever test, there was little systematic responding to the transfer cue (light) in the chain test. Rats had been trained with two different FI values in the presence of the chain, making it unlikely that chain-related cues would have gained discriminative control. To the extent that the FI 32-s signal (light) had become associated with a time of reinforcement, rats should have shown transfer in the presence of the chain (peaking close to 32 s). The fact that they did not could be taken to imply that the FI 32-s signal did not become associated with a time of reinforcement. On the other hand, it is possible that such learning did occur but could not transfer across responses.

In addition to the present study, only one other peak-procedure experiment employing more than one target response has been reported (Meck, 1984). In this study, rats could respond on either of two concurrently present levers and were trained with two signals that indicated not only a particular FI schedule but also which lever to press. A light indicated an FI 10-s schedule for responding on the left lever, and a noise indicated an FI 30-s schedule for responding on the right lever. In addition, each trial was cued by a 1-s long cue of the same modality as the subsequent trial signal and which preceded presentation of the trial signal by a brief (variable) delay. Once rats had learned to respond appropriately during each trial, test trials were given in which cue-signal pairs were recombined: The visual cue was followed by the auditory signal and the auditory cue was followed by the visual signal. On these test trials, rats responded appropriately to the cue, not the signal. On test trials with the visual cue followed by the auditory signal, rats responded on the left lever with a pattern appropriate for an empty trial with the FI 10-s visual signal, and, on test trials with the auditory cue followed by the visual signal, rats responded on the right lever with a pattern appropriate for an empty trial with the FI-s 30 auditory signal (except that on these trials, peak time was slightly delayed). Although not the interpretation chosen by the investigator, these results are understandable in terms of retrieval of a reference memory value by manipulandum cues or behavioral chaining. During training, the 1-s cue stimulus gained control over approach to the appropriate manipulandum; distinctive manipulandum cues (e.g., location) then retrieved a value from reference memory (or evoked a behavioral chain), and the role of the subsequent signal was simply to close the switch between the pacemaker and accumulator (or to initiate performance).

The present experiment attempted to investigate what cues control responding as a result of training on the peak procedure. We suggest that response-related cues play an important role in that they may retrieve information from reference memory and/or act as discriminative stimuli for subsequent behavior. In addition, response-related cues may overshadow explicit stimuli. Explicit stimuli may gain primary control over retrieval only if the validity of contextual or response-pro-

duced cues is undermined via differential training (as in the chain training sessions). Even in this case, those signals may not become potent enough to override contextual associations established at other times (as in lever-transfer sessions). It may be that the kind of transfer we had originally envisioned (i.e., peaks at 8 and 128 s when the auditory stimuli were presented for the first time with the lever) requires both reducing the validity of the manipulandum or response-produced cues present when the transfer stimuli are originally trained (e.g., the chain-related cues) and reducing the validity of the manipulandum cues present when performance to the transfer stimuli is ultimately tested (e.g., the lever-related cues).

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Received February 26, 1990

Final acceptance August 23, 1990